

Basicranial anatomy of the giant viverrid from 'E' Quarry, Langebaanweg, South Africa

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Abstract

Crania of large viverrid carnivorans (Order Carnivora, Family Viverridae) from the Upper Siwaliks of southern Asia and from Langebaanweg in South Africa indicate the presence of two evolving lineages of giant hypercarnivorous civets (*Viverra leakeyi* Petter, *Vishnuictis durandi* Pilgrim) in the Plio-Pleistocene of the Old World. Recent discovery of a cranium from Langebaanweg in 1979 and restudy of the Siwalik skulls in the British Museum demonstrate that both lines possessed typical viverrid basicranial and bullar anatomy. A third lineage of these large civets is documented by earlier discoveries at Olduvai (Tanzania) of teeth of a large hypocarnivorous viverrid (*Pseudocivetta ingens* Petter). Thus, Plio-Pleistocene faunas of Asia and Africa incorporated diverse large viverrids no longer viable in present environments yet once important as predators and omnivores in the late Cenozoic of these regions.

Introduction

In the late Cenozoic of Africa and Asia, giant viverrid carnivorans are known from dentitions and partial skulls, some discovered in the mid-nineteenth century yet never adequately described or illustrated. The basicranial anatomy of these animals has not been reviewed to determine if the auditory bulla and middle-ear structure are preserved, and to what extent these features provide insight into phylogenetic relationships.

Giant viverrids probably attained body weights of 20 to 40 kg and have been primarily reported from East and South Africa, the Siwaliks of Asia, and the Zhoukoudian travertine of China. Rare European dental remains of these large carnivores also were described by Kretzoi and Fejfar (1982)

from Villafranca d'Asti (Italy) and Ivanovce 1 (Czechoslovakia). They were first made known by fossil crania from the Siwalik Hills given by Falconer and Cautley to the British Museum and mentioned by Falconer in 1868. Subsequently, Bose (1880), Lydekker (1884), and Pilgrim (1932) described these crania. Very little information on basicranial structure was provided in these studies; referral to Viverridae rested on dental traits.

The Siwalik crania remained the only evidence of these giant viverrids until the 1960s, when research in the East African rift led to the discovery of Pliocene viverrids from Laetoli in Tanzania. Petter (1963) reported both herpestids and viverrids from Laetoli, and described the partial upper dentition of a single individual of a large viverrid which she named *Viverra leakeyi*. This was the first record of a species of *Viverra* from Africa, the genus today restricted to Asia. Since Petter's original description of the Laetoli viverrid, *V. leakeyi* has been found in the Omo Basin (Howell and Petter, 1979; Petter, 1987; Petter and Howell, 1977) of East Africa and at Langebaanweg in South Africa (Hendey, 1974).

None of the African discoveries included basicranial material. The East African fossils were primarily fragmentary dental remains, whereas the Langebaanweg sample was more representative but lacked a complete cranium. Hendey (1974) described from 'E' Quarry at Langebaanweg fragmentary cranial, postcranial, and dental remains of a large civet-like carnivoran. He referred these fossils to *Viverra leakeyi*, noting similarities to Petter's holotype, the upper teeth from Laetoli. Since Hendey's study of this material, new specimens of the giant Langebaanweg viverrid have been discovered, including a magnificent complete cranium and associated mandibles (South African Museum LBW 1979 PQ-L51590) found in 1979. My colleague C.S. Churcher and his student Grant Hurlburt are describing this cranium. I thank them for the invitation to discuss the basicranial anatomy of the animal and to comment on its relevance to the Siwalik crania in the Falconer collection of the British Museum (Natural History), London, which I have recently been able to examine through the courtesy of Dr Alan Gentry.

The Langebaanweg viverrid cranium

The cranium and mandible (Fig. 1) are nearly complete, and reveal a gracile, dolichocephalic carnivoran much different from the skull form of the Siwalik giant viverrids. The cranium in fact is remarkably similar to that of living species of *Viverra*, particularly in its elongate rostrum and sloping forehead. The size of the animal is indicated by its basilar length, 20.2 cm. Despite breakage and bone missing in the orbital region, the skull includes nearly the entire dentition and a well-preserved basi-



FIGURE 1. Cranium and associated mandible of the giant viverrid *Viverra leakeyi* from 'E' Quarry, Langebaanweg, South Africa (South African Museum no. PQ-L51590) (basilar length of skull, 20.2 cm; scale in mm; the basicranial anatomy of this skull is shown in Fig. 3)

cranium. It was found at 'E' Quarry in the Pelletal Phosphorite Member of the Varswater Formation (Hendey, 1974; Tankard, 1974), considered Pliocene in age.

The dentition of this carnivoran is sectorial, having a well-developed shearing upper carnassial, a triangular M1, reduced and smaller M2 (no M3), and laterally compressed yet robust premolars. The canines are conical, slightly recurved, stabbing teeth. Based upon the cranium and limited postcranial material, a restoration of the Langebaanweg *Viverra* has been created to suggest a carnivorous predator able to actively pursue prey in a variety of environments (Fig. 2).

The nature of the dentition is important, distinguishing the Langebaanweg carnivoran from the large crushing-toothed viverrid *Pseudocivetta ingens*, described by Petter (1965, 1967) from Olduvai Gorge in Tanzania, and later found in the Omo Basin (Petter and Howell, 1977). The strong contrast between the dentitions of these two animals demonstrates their separate identity and thus the presence of at least two large viverrids in Africa in the Plio-Pleistocene.

Basicranium of the Langebaanweg viverrid

Although only a fragment of the auditory bulla is present, the basicra-

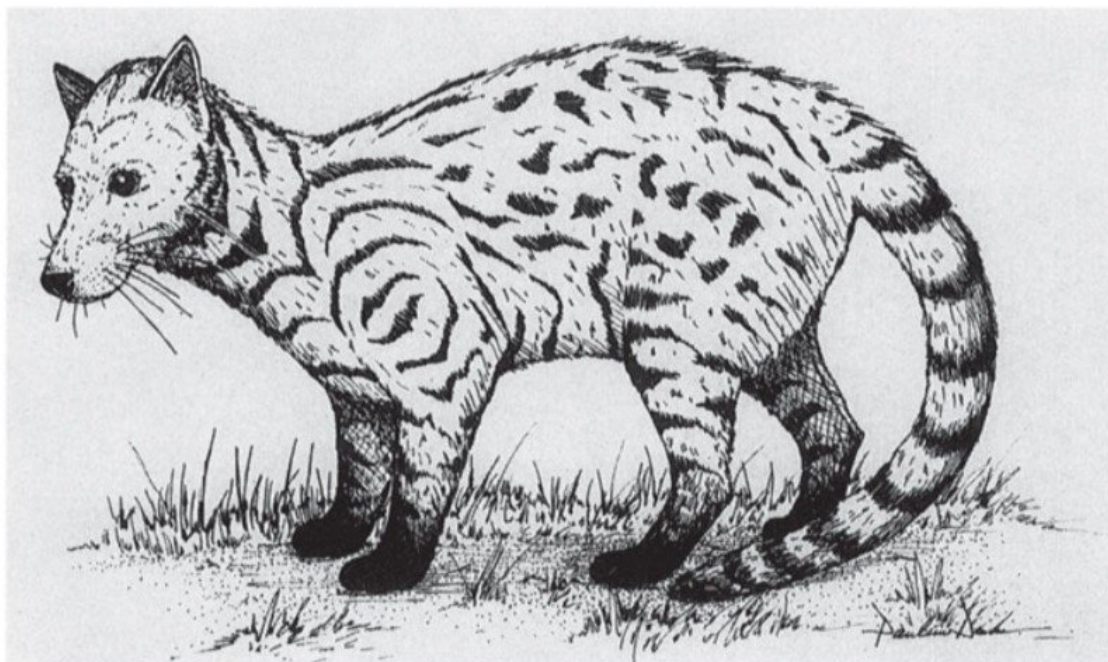


FIGURE 2. Restoration of the giant African viverrid *Viverra leakeyi* based on the fossil material from Langebaanweg, South Africa

nium is otherwise nearly intact (Fig. 3A, B). The middle-ear cavity, petrosal, and surrounding bones of the basicranium are unequivocally viverrid in form, and confirm Hendey's (1974) inference as to the viverrid affinity of this material. Although the bulla is almost entirely lost from the skull, the form of the squamosal, alisphenoid, basioccipital, and exoccipital demonstrate that the viverrid bipartite bulla was fully developed as in living Viverridae. The bulla was enormous and therefore susceptible to breakage. Only part of the ectotympanic is preserved in the right auditory region, and is similar in form to the modern viverrid ectotympanic that houses the anterior chamber of the bulla. The anterior crus of the ectotympanic rests in a deep pit in the squamosal, and the posterior crus although broken away must have contacted the post-tympanic process of the squamosal. Only limited development of an external auditory bony meatus occurs in the fossil just as in living viverrids. Posterior to the ectotympanic fragment, the expanded paroccipital process of the exoccipital bone and the conspicuous impressions on the margins of the basioccipital indicate an expanded viverrid caudal entotympanic of considerable volume as seen in *Viverra* and *Civettictis*. The height of the paroccipital process when compared to the height of the ectotympanic fragment shows that the caudal entotympanic chamber undoubtedly extended forward over the smaller subordinate anterior chamber of the bulla, producing a bulla configuration as in living viverrids.

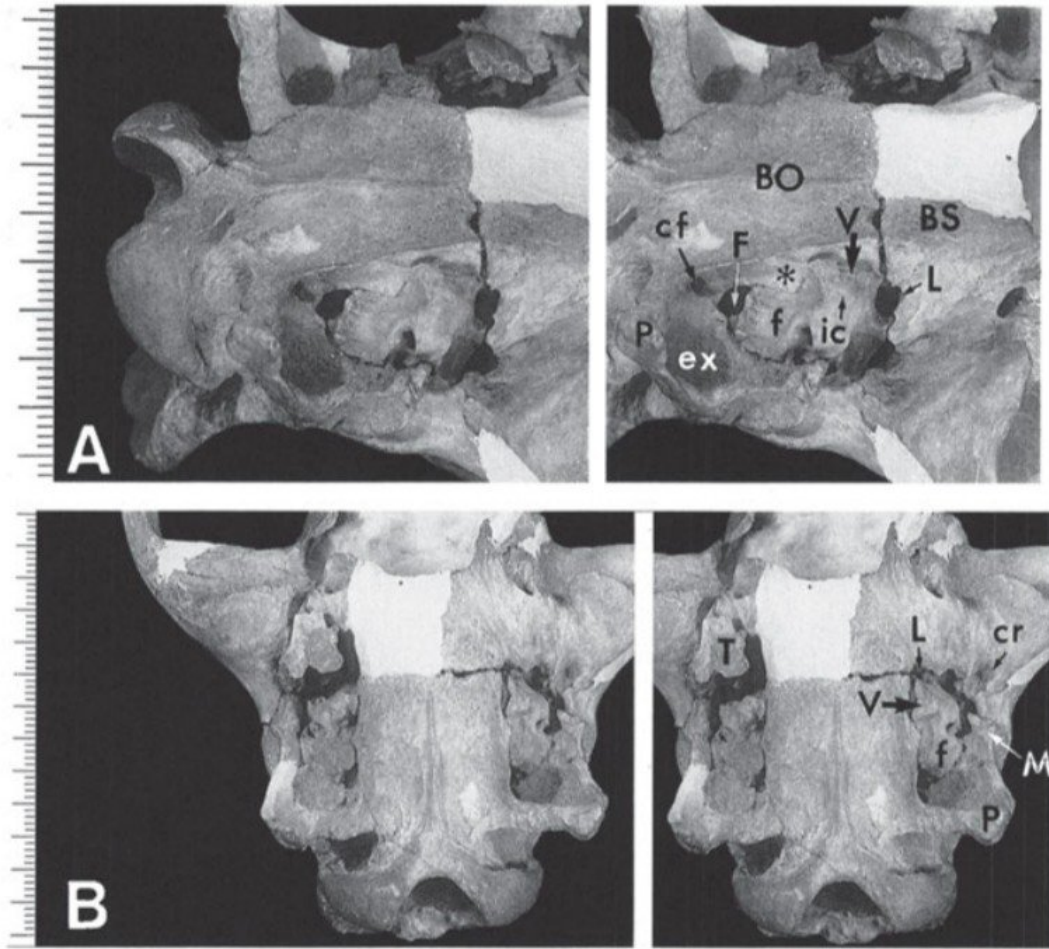


FIGURE 3. A. Basicranium and left auditory region of the giant civet *Viverra leakeyi* in ventrolateral view (same individual as Figure 1). The auditory bulla is missing from the left side, revealing the petrosal, middle ear, and surrounding bones. The petrosal is of the aeluroid type, with a prominent ventral promontorial process (V) and a lateral groove for the internal carotid artery (ic). The paroccipital process (P) is expanded to receive the enlarged caudal entotympanic chamber of the auditory bulla. Note the expanded exoccipital (ex) to accommodate the inflated caudal entotympanic element. The lateral margin of the basioccipital also is impressed by the medial wall of the caudal entotympanic, creating the small depression (*) posterior to the ventral promontorial process. A prominent flange (f) of the petrosal extends in a posterior direction from the promontorium to the posterior lacerate foramen (F). The condyloid foramen (cf) is situated behind the posterior lacerate foramen. The middle lacerate foramen (L) occurs just dorsal to the basioccipital (BO)-basisphenoid (BS) suture.

B. Ventral view of the basicranium (same individual as Figure 3A), partial ectotympanic (T) present in the anterior part of the right auditory region. A prominent pit (cr) for the anterior crus of the ectotympanic is evident in the squamosal when the bulla is removed in the left auditory region. The mastoid process (M) is only moderately developed. (Other abbreviations as in Figure 3A; scale in mm; stereopairs)

A typical aeluroid petrosal of viverrid type is present in the Langebaanweg cranium (Fig. 3A). The left petrosal is most complete and displays a prominent ventral promontorial process diagnostic for aeluroid Carnivora (compare Hunt, 1989: Fig. 1A). Only the tip of the process has been lost; this tip protruded ventrad in life between basioccipital and the bulla's medial wall as in living civets. The process lies just posterior to the basisphenoid-basioccipital suture and is grooved on its lateral face for the internal carotid artery. Posterior to the promontorium the petrosal is extended backward as a broad flange that forms the anterior border of the posterior lacerate foramen. In some modern viverrids such as *Civettictis* the flange is present but is not as developed, leaving a space behind the petrosal that is completely filled in the Langebaanweg skull by bone. The condyloid foramen is recessed within the space for the posterior lacerate foramen, and the postglenoid foramen is lost, indicating that venous drainage has been redirected through the posterior lacerate pathway (internal jugular vein) as in living viverrids and other aeluroids. The mastoid process is only moderately developed. In all respects, the auditory region and the inferred form of the bulla are typical of living Viverridae.

The Siwalik viverrid crania

The Siwalik crania were originally described by Lydekker (1884) and Pilgrim (1932), although Falconer included mention of some specimens in his palaeontological memoir of 1868. Here I consider as giant Siwalik viverrids only the lineage named *Vishnuictis* by Pilgrim (1932:101–108). Pilgrim included in this lineage a cranium and associated mandible of moderate size from the Dhok Pathan 'stage' which he made the genoholotype, *Vishnuictis salmontanus*. He also referred to *Vishnuictis* the largest viverrid crania known from the Siwalik Hills, presumed to have come from the Pinjor 'stage' of Plio-Pleistocene age, placing them in a new species, *V. durandi* (Fig. 4). Both species of *Vishnuictis* are represented by crania extremely similar to each other in form and different in this respect from the Langebaanweg cranium. As noted by Pilgrim, the Siwalik *Vishnuictis* have expanded frontal regions, marked postorbital constrictions, relatively short rostra, with deep maxillae. They are much more like the living *Civettictis* in skull form than like *Viverra*. It seems probable that the two species are a lineage, *V. salmontanus* the earlier form, *V. durandi* the descendant.

Two crania from the Pinjor Siwaliks were initially described as belonging to *Vishnuictis durandi*: the holotype, BM(NH) M1338 (Fig. 4B), and a referred rostrum without basicranium, BM(NH) M37150 (Fig. 4C). The holotype preserves the basicranium and auditory bulla, although damaged to a degree, and retains a partial dentition, whereas the referred

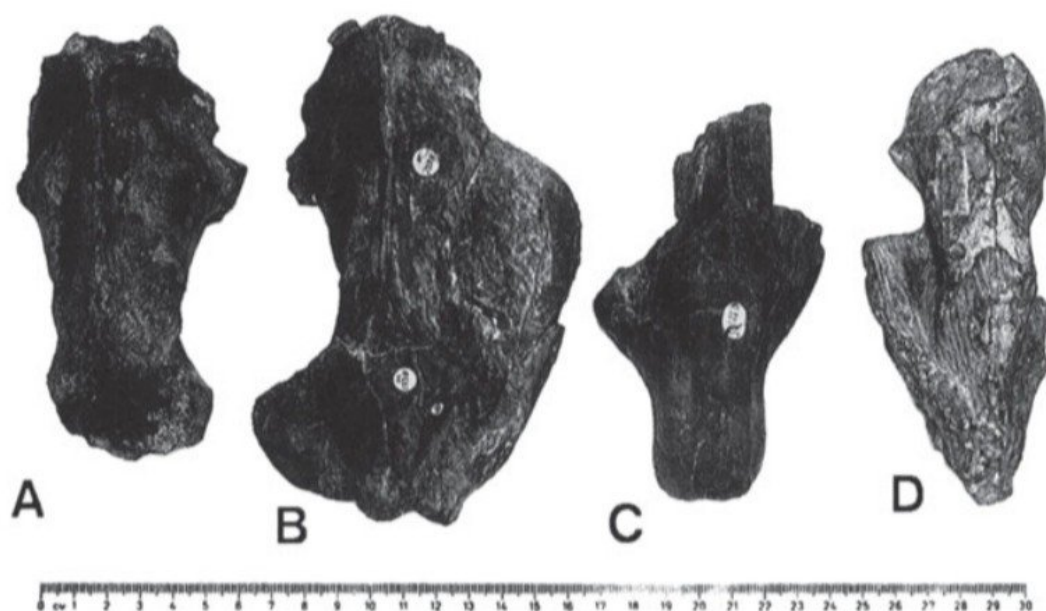


FIGURE 4. Crania in dorsal view of the large Siwalik civet *Vishnuictis durandi* Pilgrim (A, M37131; B, M1338; C, M37150) and the smaller Siwalik viverrid *Viverra bakeri* Bose (D, M40183) conserved in the palaeontological collections of the British Museum (Natural History), London. Basicranial anatomy and teeth are preserved in M1338, the holotype cranium of *Vishnuictis durandi*. Note the expanded frontal region and short, deep rostrum in *Vishnuictis*. (Scale in mm)

rostrum lacks teeth. As Pilgrim suggested, they surely belong to a single species; in fact, the holotype lacks the rostrum which is contributed by the referred M37150, allowing a complete reconstruction of the cranium to be made. During my study of the Siwalik collection of Falconer and Cautley at the British Museum, I encountered a third partial cranium (Fig. 4A), BM(NH) M37131, that also can be referred to *V. durandi*. There is no locality data with this skull, but the preservation is similar to the other two crania. It is a posterior cranium complete as far forward as the frontal region, but lacks the rostrum and teeth entirely. These three crania have estimated basilar lengths of 18–20 cm, and thus are similar in length to the Langebaanweg viverrid. There are, however, significant differences that preclude referral to the same species, and indicate that these are separate lineages.

The Siwalik crania of *Vishnuictis* have markedly expanded frontal regions, so much so that the frontal expansion slopes downward to the smaller braincase. In the Langebaanweg skull the frontal region is not expanded and the forehead slopes upward to the braincase (Fig. 1). The Langebaanweg viverrid also has a long narrow rostrum and shallow maxillae, in contrast to the robust massive rostra and deep facial region of

the Siwalik viverrids. In the dentition both Siwalik *Vishnuictis* and Langebaanweg *Viverra* are hypercarnivorous, sectorial forms in the construction of the carnassial and molars. But the holotype of *V. durandi*, which is the only cranium to preserve the teeth of this species, shows a more sectorial carnassial-molar region than seen in the Langebaanweg species. One might suppose that the dentition and skull form of *Vishnuictis durandi* are derived features evolved from an animal like the Pliocene Langebaanweg viverrid, but this is unlikely given the existence in the Dhok Pathan sediments of the smaller yet already specialized *Vishnuictis salmontanus*. Consequently, it seems that the Siwalik *Vishnuictis* and Langebaanweg *Viverra* lines are distinct and separate, and indicate the presence of two large hypercarnivorous viverrid lineages in the Plio-Pleistocene of the Old World.

In two of the Siwalik crania (M1338, M37131) the basicranium is preserved. The left auditory bulla survives in the holotype skull, although somewhat damaged. It displays a typical viverrid bulla configuration in which an expanded caudal entotympanic chamber anteriorly overgrows the smaller ectotympanic element. In M37131 the bulla is also preserved on the left side and is similar in what remains to that of M1338. Thus, the Siwalik giant viverrids possess typical viverrid auditory regions and, despite the differences in skull form and teeth between the Siwalik and Langebaanweg lineages, the auditory bulla pattern is similar and definitely of the viverrid type.

It was possible to examine another smaller viverrid from the Siwalik Hills during my visit to the British Museum. The holotype skull (Fig. 4D) was presumed by Pilgrim (1932) to have also come from the Pinjor 'stage' of the Upper Siwaliks (Siwalik Hills). This is the cranium of *Viverra bakeri*, BM(NH) M40183, originally described by Bose in 1880, and later discussed by Lydekker (1884). Basilar length of skull is about 14 cm, much smaller than in *Vishnuictis durandi*. Lydekker, Pilgrim, and later workers agreed that *Viverra bakeri* is a different lineage relative to *Vishnuictis*, and this is supported by the form of the upper teeth, particularly the molars which show additional cuspatation and some enlargement, indicating a possible trend towards a more crushing dentition. Matthew (1929) suggested that the teeth of *V. bakeri* are adapting to a less carnivorous diet and I would concur, regarding this species as a small viverrid evolving towards hypocarnivory but still retaining a moderately sectorial dentition. Its basicranium is too poorly preserved to determine its structure, but the general form and the dentition indicate this is also a viverrid.

Acknowledgments

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